

Thermoregulation and torpor in African woodland dormice, *Graphiurus murinus*, following cold acclimation

By G. T. H. ELLISON and J. D. SKINNER

Mammal Research Institute, University of Pretoria, Pretoria, South Africa

Receipt of Ms. 28. 11. 1989

Acceptance of Ms. 14. 9. 1990

Abstract

Studied thermoregulation of 3 adult woodland dormice (*Graphiurus murinus*) following acclimation to 15 °C and 10 °C. The dormice entered hibernation under these conditions characterised by a fall in body temperature to within 1 °C of ambient, and a prolonged reduction in oxygen consumption measured over 24 h at 10 °C and 5 °C. Non-shivering thermogenic capacity exceeded that required to re-attain homeothermy by 20 %, but would permit these dormice to maintain normothermia down to -5 °C. The cycle of body mass displayed by *G. murinus* in the present study is characteristic of hibernating temperate dormice, but was not observed in specimens collected throughout the year in southern Africa. It therefore appears that woodland dormice may not enter hibernation throughout their distribution during winter, but may exhibit facultative torpor under adverse climatic conditions.

Introduction

African woodland dormice, *Graphiurus murinus*, are small, arboreal rodents found throughout large areas of tropical and subtropical Africa (SMITHERS 1983). Although EISENTRAUT (1962) could not elicit torpor in *G. murinus* from West Africa (Cameroon), SMITHERS (1983) suggested that this species shows signs of lethargy during cold weather in South Africa. Following the discovery of a torpid woodland dormouse during rodent trapping by the authors outside Pretoria in March 1987, the following study was initiated to investigate thermoregulation and torpor in *G. murinus* under controlled laboratory conditions.

Material and methods

Three African woodland dormice (2 adult females, 1 adult male) were collected at Vaalkop Dam Nature Reserve (25°23' 27°28' E) during April 1989. Within one week of capture the dormice were transferred to a windowless climate chamber (Specht Scientific, Johannesburg) at Pretoria University (25°45' S 28°12' E) wherein photoperiod and temperature could be accurately controlled. Throughout the study the photoperiod within the chamber was maintained at 10 h light : 14 h dark (lights on at 07h00 and off at 17h00) which closely resembled the photoperiod prevailing at Vaalkop Dam during mid-winter. The dormice were initially acclimated for 50 days at an ambient temperature (T_a) of 15 °C followed by a further 50 days at $T_a = 10$ °C. The dormice were housed separately in standard laboratory rat cages containing sawdust, shredded paper and a 500 ml plastic beaker which served as a nest box. Water, sunflower seeds, rat cubes and rabbit pellets (Epol, Vereniging) were provided ad libitum, a diet occasionally supplemented with pieces of fresh apple.

The body mass of each dormouse was recorded upon capture and subsequently at regular intervals throughout the study. In addition, rectal temperatures (T_b) were measured between 07h00-13h00 on five occasions during acclimation to both $T_a = 15$ °C and $T_a = 10$ °C. T_b was determined by inserting a chromel alumel thermocouple (K-Type: Fluke, Everett), attached to a digital thermometer, approximately 2 cm into the rectum for a period not exceeding 15 sec. To avoid undue perturbation, body mass and rectal temperature were recorded at intervals of 3 days or more, and at all other times the dormice remained undisturbed within the climate chamber.

Following 50 days acclimation at 10 °C the oxygen consumption ($\dot{V}O_2$) of the dormice was measured as an indication of metabolic rate (MR) using an open-circuit system (as described by DEPOCAS and HART 1957, and HILL 1971). The dormice were placed in perspex metabolic chambers

through which a flow of dried air (Silica Gel: Holpro, Johannesburg) was passed at a rate of $600 \text{ ml} \times \text{min}^{-1}$. The chambers were immersed in a constant temperature water bath (Labotec, Isando), and a chromel alumel thermocouple within the chamber was used for monitoring chamber temperature (T_c). Following full equilibration $\dot{V}O_2$ was recorded using an Ametek S-3A/1 oxygen analyser (Applied Electrochemistry, Pittsburgh) linked to a multi-channel data logger (Grant Instruments, Cambridge). The oxygen analyser was calibrated before and after measurement, and $\dot{V}O_2$ was corrected to standard temperature and pressure, dry (STPD).

Average daily metabolic rate (ADMR) was measured over 48 h in large (13 l) metabolic chambers. The dormice were transferred to these chambers, together with their bedding and food, 20 h prior to the start of measurement, and were subsequently subjected to 24 h at $T_c = 10^\circ\text{C}$ followed by 24 h at $T_c = 5^\circ\text{C}$. Air leaving the chambers was connected to a three-way valve and time-switch (Air/Water 350 KPA: Ascoreg, Johannesburg), so that $\dot{V}O_2$ from two dormice could be monitored simultaneously every 30 min using a single oxygen analyser. At the end of measurement the mass and rectal temperature of each dormouse was recorded.

Resting metabolic rate (RMR) was measured following one hour's exposure to $T_c = 5^\circ\text{C}$ and 10°C within smaller metabolic chambers (700 ml). $\dot{V}O_2$ was monitored over 30 min after which rectal temperature and body mass were recorded.

Maximum oxygen consumption ($\dot{V}O_{2\text{max}}$) following an injection of noradrenaline (NA) was used as an indication of non-shivering thermogenetic capacity (as described by HELDMAIER 1971). The dormice were anaesthetised with sodium pentobarbitone (70 mg/kg intraperitoneally. Sagatal: Maybaker, Port Elizabeth) after which a chromel alumel thermocouple (J-Type: Grant Instruments, Cambridge) was inserted deep into the rectum to measure T_b and secured to the base of the tail with tape. Following a subcutaneous injection of 1.5 mg/kg NA (HELDMAIER 1971) the dormice were transferred to a small metabolic chamber (700 ml) at $T_c = 30^\circ\text{C}$ and $\dot{V}O_2$ and T_b were recorded simultaneously at one minute intervals for 60 min using the multichannel data logger. $\dot{V}O_{2\text{max}}$ and $T_{b\text{max}}$ were taken as the highest values of $\dot{V}O_2$ and T_b recorded following NA injection.

All results are presented as mean \pm one standard deviation unless otherwise stated.

Results

Body mass

Following acclimation, the mean body mass of dormice in the present study entered a cycle comprising a rapid period of weight gain followed by a slower sequence of weight loss. From a mean capture mass of 29.1 ± 4.3 g the dormice weighed 43.2 ± 4.3 g after 25 days in captivity, an increase of almost 50 %. Following a gradual decline the dormice returned to capture mass by Day 65, after which they retained a stable mean body mass for the remainder of the study.

Body temperature

All the measurements of T_b taken during acclimation to $T_a = 15^\circ\text{C}$ and 10°C were pooled and displayed in two histograms (Fig. 1). Under both T_a regimes the dormice were predominantly torpid, with the majority of T_b measurements falling at, or slightly above T_a . At these T_b s the dormice were stiff and displayed the lack of responsivity and coordination characteristic of deep torpor. In addition, the level of hypothermia recorded was dependant upon T_a , being lower at $T_a = 10^\circ\text{C}$ than at $T_a = 15^\circ\text{C}$. Few T_b measurements fell within the normothermic range for mammals (33°C – 36°C) which suggests that the dormice were usually in torpor between 07h00 and 13h00 when T_b was recorded.

Metabolism

At 10°C the mean RMR of the dormice was $3.74 \pm 0.14 \text{ mlO}_2 \times \text{g}^{-1} \times \text{h}^{-1}$ ($T_b = 34.7 \pm 0.4^\circ\text{C}$) and increased slightly at 5°C to $3.99 \pm 0.15 \text{ mlO}_2 \times \text{g}^{-1} \times \text{h}^{-1}$ ($T_b = 34.1 \pm 0.1^\circ\text{C}$). In contrast, $\dot{V}O_2$ measured over 24 h at these temperatures remained at low levels for prolonged periods, punctuated with brief increases in $\dot{V}O_2$ lasting between 1 h and 6 h (Fig. 2). Excluding these incidents of increased metabolism, the mean ADMR

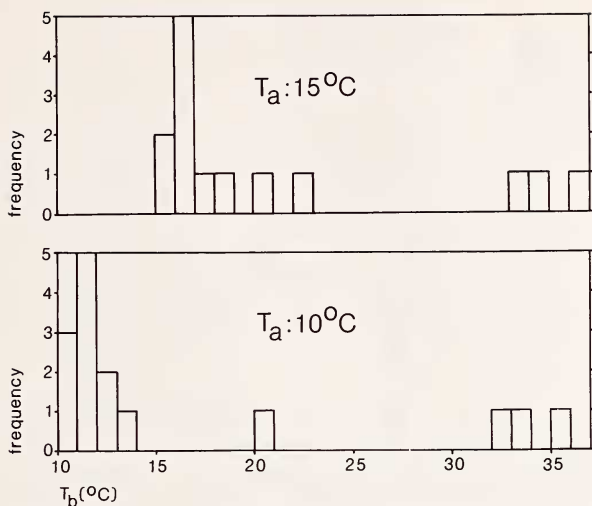


Fig. 1. Rectal temperatures recorded between 07h00 and 13h00 during acclimation to $T_a = 15^\circ\text{C}$ and 10°C

at 10°C ($0.27 \pm 0.06 \text{ mlO}_2 \times \text{g}^{-1} \times \text{h}^{-1}$) was only 7.3 % RMR and at 5°C ($0.52 \pm 0.26 \text{ mlO}_2 \times \text{g}^{-1} \times \text{h}^{-1}$) was 13.0 % RMR (Fig. 3). Despite the modest rise in ADMR following exposure to 5°C , the dormice exhibited a mean T_b of $6.0 \pm 0.3^\circ\text{C}$ at the end of measurement.

The male dormouse died under anaesthesia during the measurement of NST, whilst the females displayed a mean $\dot{V}\text{O}_{2\text{max}}$ of $5.75 \pm 0.67 \text{ mlO}_2 \times \text{g}^{-1} \times \text{h}^{-1}$ following NA injection, accompanied by mean $T_{b\text{max}}$ of $40.6 \pm 1.0^\circ\text{C}$. When compared to ADMR and RMR in Fig. 3 $\dot{V}\text{O}_{2\text{max}}$ was found to exceed the level of heat production required to maintain normothermia at either 10°C or 5°C . However, according to HELDMAIER'S (1971) allometric equation relating $\dot{V}\text{O}_{2\text{max}}$ to body mass, the $\dot{V}\text{O}_{2\text{max}}$ recorded in the present study is approximately 90 % of that predicted for mammals of similar body size following cold (5°C) exposure ($\dot{V}\text{O}_{2\text{max}}$ predicted: $6.37 \text{ mlO}_2 \times \text{g}^{-1} \times \text{h}^{-1}$).

Discussion

The results of the present study clearly indicate that *G. murinus* from southern Africa is capable of spontaneous bouts of deep torpor when confronted with cold stress under simulated winter photoperiod. Furthermore, these bouts of torpor exceeded 24 h in duration, which suggests that *G. murinus* entered hibernation under these conditions. Hibernating dormice rarely arouse when challenged with declining temperatures and instead increase metabolic thermogenesis to maintain T_b at non-lethal levels even as T_a falls to 0°C or below (WALHOVD 1976; PAJUNEN 1986). In the present study torpid dormice displayed an increase in metabolism when T_a fell from 10°C to 5°C , which indicates that torpor in *G. murinus*, in common with other dormice, is facultative and under strict thermoregulatory control. However, a consequence of this increase in metabolic rate is that an optimal T_a exists for maximum energy savings during hibernation, as described for the garden dormouse, *Eliomys quercinus* (PAJUNEN 1986). For *G. murinus* the optimal T_a appears to fall between 10°C and 5°C which corresponds to the mean night-time temperature of around 5°C prevailing during winter (June/July) at Vaalkop Dam (Pretoria Weather Bureau: Brits Met. Stn. $25^\circ35' \text{ S } 27^\circ49' \text{ E } 1939\text{--}1984$).

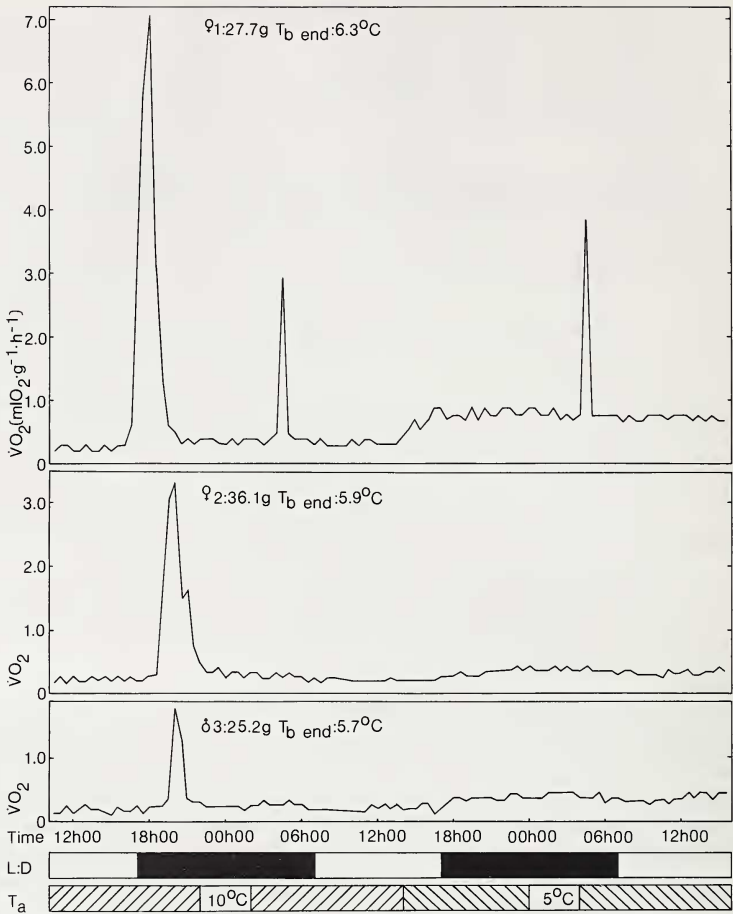


Fig. 2. Oxygen consumption ($\dot{V}O_2$) of 3 *Graphiurus murinus* measured over 24 h at 10°C and 5°C

Non-shivering thermogenesis is the dominant pathway for heat production in small mammals (BÖCKLER et al. 1988) although hibernators exhibit higher levels of NST than euthermic species of similar body size even in the absence of cold adaptation (JANSKÝ 1973). This enhanced capacity for NST amongst hibernators is believed to be associated with the heat required for arousal from hypothermia (ABBOTTS and WANG 1980). If we assume that the specific heat capacity of animal tissue is $3.4 \text{ kJ} \times \text{g}^{-1}$ (CHAPPELL and BARTHOLOMEW 1981) and that the calorific equivalent of oxygen is $20.1 \text{ J} \times \text{mlO}_2^{-1}$ (SCHMIDT-NIELSEN 1983) then rewarming a 31.9 g dormouse from $T_b = 6.1^\circ \text{C}$ to 34.4°C (28.3°C) in the present study would require 3.07 kJ or 152.74 mlO_2 . This compares with the total heat produced during NST of $5.75 \text{ mlO}_2 \times \text{g}^{-1} \times \text{h}^{-1}$ or $183.43 \text{ mlO}_2 \times \text{h}$, which exceeds that required for rewarming by 20%. For this reason NST in *G. murinus* may be important not only for arousal from hypothermia, but also for the maintenance of homeothermy in the cold. In this context the lowest T_a at which *G. murinus* can thermoregulate, using NST alone, can be calculated assuming that Newton's law of cooling holds for this species as proposed by SCHOLANDER et al. (1950): (Thermal conductance below thermoneutrality $[C_m] = \dot{V}O_2 \times [T_b - T_a]^{-1}$). Based upon RMR and T_b measured at 5°C and 10°C , the mean C_m of dormice in the present study, was 0.145 ± 0.010

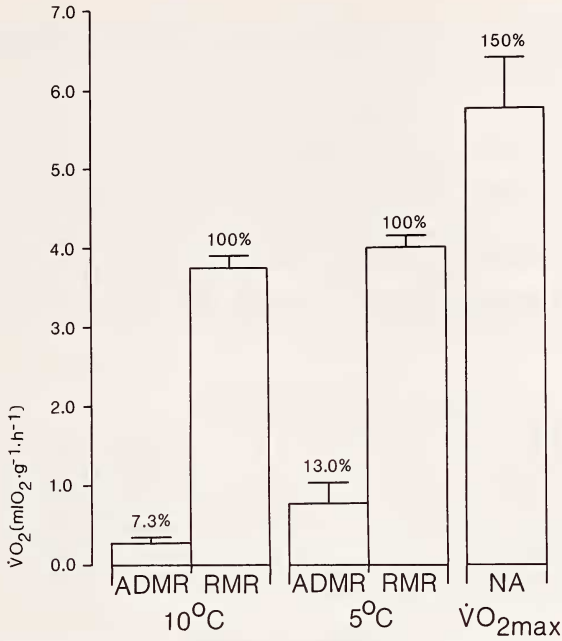


Fig. 3. The relationship between average daily metabolic rates (ADMR) during torpor and resting metabolic rate (RMR) during normothermia measured at 10°C and 5°C in 3 *Graphiurus murinus*. As an indication of non-shivering thermogenic ability, the metabolic response to noradrenaline injection (NA: $\dot{V}O_{2max}$) of 2 *G. murinus* is displayed to the right. Vertical lines indicate \pm one standard deviation of the mean

$\text{mlO}_2 \times \text{g}^{-1} \times \text{h}^{-1} \times \text{°C}^{-1}$ with a mean normothermic T_b of 34.4 ± 0.4 °C. Using NST to produce a $\dot{V}O_{2max}$ of $5.75 \text{ mlO}_2 \times \text{g}^{-1} \times \text{h}^{-1}$ these dormice could feasibly maintain a similar T_b down to T_a 's as low as -5 °C, which corresponds to the mean daily minimum temperature (-3 °C) recorded at Vaalkop Dam during winter (June/July: Pretoria Weather Bureau).

The body mass cycle displayed by *G. murinus* in the present study is similar to that reported for *Glis glis* and *E. quercinus* during winter and following cold acclimation (MROSOVSKY 1986; PAJUNEN 1986). These dormice undergo a distinct increase in body mass prior to hibernation, during which up to 25 % of body mass is subsequently lost (JALLAGEAS and ASSENMACHER 1986). In order to assess whether or not *G. murinus* displays similar body mass cycles in nature the mass of 77 specimens collected throughout the southern African subregion were grouped by month of capture and presented in the Table.

These specimens did not display a clear circannual cycle of body mass, which suggests that *G. murinus* does not naturally enter hibernation throughout southern Africa. Indeed,

Mean body mass of 77 *G. murinus* collected throughout the southern African subregion
(From the archives of the Transvaal Museum, Pretoria)

Month	Jan/Feb	Mar/Apr	May/June	Jul/Aug	Sep/Oct	Nov/Dec
Mass	21.6 g	22.5 g	25.0 g	23.6 g	23.7 g	22.5 g
S.D.	± 8.3 g	± 8.5 g	± 8.5 g	± 4.4 g	± 5.9 g	± 7.0 g
n	21	22	6	9	13	6

the cycle of body mass observed in the present study may have been an artefact of laboratory conditions as both short photoperiod (KÖNIG 1960) and abundant food (ROTHWELL and STOCK 1986) have been reported to elicit increased body mass and subsequent hibernation in other species of dormice. However, under similar conditions, EISENTRAUT (1962) could not elicit torpor or hibernation from *G. murinus haedulus* from tropical West Africa which suggests that different populations of this species differ in their ability to display torpor and/or hibernate. Similar geographic differences have been reported for forest dormice (*Dryomys nitedula*) which hibernate for 6 months in Eurasia yet remain active throughout the year in Israel (NEVO and AMIR 1964). It therefore appears that *G. murinus* from southern Africa differ from tropical populations in their ability to enter deep torpor/hibernation, although, like garden dormice in Morocco, this ability is probably only expressed when local climatic conditions demand (MORENO and DELIBES 1964).

Acknowledgements

The authors would like to thank BABSIE POTGIETER for providing excellent technical assistance throughout the study and AMY and NICK BEZUIDENHOUT for their generous hospitality at Vaalkop Dam. INGO BUCHERT, GUSTAV PETERS, WOLFGANG RAMDOHR and BRIGITTE WENHOLD kindly helped with german translation and assisted in collating the final manuscript. Collection data was provided by the Mammal Department at the Transvaal Museum, and climatic information was supplied by the Weather Bureau in Pretoria. G.T.H.E. was supported by grants from the Foundation for Research Development, Department of National Education, and University of Pretoria.

Zusammenfassung

Thermoregulation und Torpor bei afrikanischen Baumschläfern, Graphiurus murinus, nach Kältebelastung

Zahlreiche Arten der Gliridae aus den gemäßigten Klimazonen sind Winterschläfer. Über einen saisonbedingten Torpor bei Baumschläfern (*Graphiurus murinus*) aus den tropischen und subtropischen Gegenden Afrikas liegen nur Vermutungen vor. Drei erwachsene *G. murinus* wurden im Herbst im südlichen Afrika gefangen und im Labor 50 Tage lang bei 15 °C und 10 °C sowie unter kurzer Lichtperiode gehalten. Sie gerieten dabei in Torpor. Die Körpertemperaturen sanken bis auf den Wert der Umgebungstemperatur. Die durchschnittliche Stoffwechsellintensität fiel bei 10 °C und 5 °C bis auf 7,3 % bzw. 13,0 % des Ruhewertes im normothermen Zustand. Die durch Noradrenalin induzierte zitterfreie Thermogenese übertraf die für das Erwachen aus dem Torpor benötigte Wärme. Die Bilche reagierten auf die Kältebelastung mit einer Gewichtszunahme und mit nachfolgendem Gewichtsverlust. Tiere, die im Verlaufe des Jahres gefangen wurden, zeigten diesen Zyklus nicht. Vermutlich gibt es bei *G. murinus* nur unter sehr ungünstigen klimatischen Bedingungen Torpor.

References

- ABBOTTS, B.; WANG, L. C. H. (1980): Seasonal thermogenic capacity in a hibernator, *Spermophilus richardsonii*. J. Comp. Physiol. B. 140, 235–240.
- BÖCKLER, H.; STEINLECHNER, S.; HELDMAIER, G. (1982): Complete cold substitution of noradrenaline induced thermogenesis in the Djungarian hamster, *Phodopus sungorus*. Experientia 38, 261–262.
- CHAPPELL, M. A.; BARTHOLOMEW, G. A. (1981): Activity and thermoregulation in the antelope ground squirrel *Ammospermophilus leucurus* in winter and summer. Physiol. Zool. 54, 215–223.
- DEPOCAS, F.; HART, J. S. (1957): Use of the Pauling oxygen analyser for measurements of oxygen consumption of animals in open-circuit system and in short-lag, closed-circuit apparatus. J. Appl. Physiol. 10, 388–392.
- EISENTRAUT, M. (1962): Wie verhalten sich verwandte Vertreter von heimischen Winterschläfern aus wärmeren Gebieten unter veränderten Temperaturbedingungen? Zool. Anz. 169, 429–432.
- HELDMAIER, G. (1971): Zitterfreie Wärmebildung und Körpergröße bei Säugetieren. Z. vergl. Physiol. 73, 222–248.
- HILL, R. W. (1972): Determination of oxygen consumption by use of the paramagnetic oxygen analyser. J. Appl. Physiol. 33, 261–263.
- JALLAGEAS, M.; ASSENMACHER, I. (1986): External factors controlling hibernation and related endocrine cycles in the edible dormouse, *Glis glis*. In: Endocrine regulations as adaptive

- mechanisms to the environment. Ed. by I. ASSENMACHER and J. BOISSIN. Paris: Editions du Centre National de la Recherche Scientifique. Pp. 363–369.
- JANSKY, L. (1973): Non-shivering thermogenesis and its thermoregulatory significance. *Biol. Rev.* **48**, 85–132.
- KÖNIG, C. (1960): Einflüsse von Licht und Temperatur auf den Winterschlaf des Siebenschläfers *Glis glis* (Linnaeus 1766). *Z. Morph. Ökol. Tiere* **48**, 545–575.
- MORENO, S.; DELIBES, M. (1982): Notes on the garden dormouse (*Eliomys*; Rodentia, Gliridae) of northern Morocco. *Säugetierkd. Mitt.* **30**, 212–215.
- MROSOVSKY, N. (1986): Mirrors of the environment: the enigmatic dormouse and other hibernators. In: Endocrine regulations as adaptive mechanisms to the environment. Ed. by I. ASSENMACHER and J. BOISSIN. Paris: Editions du Centre National de la Recherche Scientifique. Pp. 331–341.
- NEVO, E.; AMIR, E. (1964): Geographic variation in reproduction and hibernation patterns of the forest dormouse. *J. Mammalogy* **45**, 69–87.
- PAJUNEN, I. (1986): Ambient temperature dependence of physiological parameters during long-term hibernation in the garden dormouse, *Eliomys quercinus*. In: Endocrine regulations as adaptive mechanisms to the environment. Ed. by I. ASSENMACHER and J. BOISSIN. Paris: Editions du Centre National de la Recherche Scientifique. Pp. 379–383.
- ROTHWELL, N. J.; STOCK, M. J. (1986): Spontaneous and experimental variations in body weight, food intake and metabolic rate in captive dormice (*Glis glis*). *Comp. Biochem. Physiol.* **84A**, 141–147.
- SCHMIDT-NIELSEN, K. (1983): Animal physiology: Adaptation and environment. 3rd ed. Cambridge: Cambridge University Press. Pp. 178.
- SCHOLANDER, P. F.; WALTERS, V.; HOCK, R.; IRVING, L. (1950): Body insulation of some arctic and tropical mammals and birds. *Biol. Bull.* **99**, 237–258.
- SMITHERS, R. H. N. (1983): The mammals of the southern African subregion. Pretoria: Univ. Pretoria.
- WALHOVD, H. (1976): Partial arousals from hibernation in a pair of common dormice, *Muscardinus avellanarius*, (Rodentia, Gliridae), in their natural hibernaculum. *Oecologia (Berl.)* **25**, 321–330.
- Authors' address:* G. T. H. ELLISON, and J. D. SKINNER, Mammal Research Institute, University of Pretoria, Pretoria 0002, Republic of South Africa